

***MALDANE CALIFORNIENSIS*, A NEW SPECIES
(POLYCHAETA: MALDANIDAE)
AND A REVIEW OF ITS RELATIONS**

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ABSTRACT

Maldene californiensis is described from deep waters (about 85 m to 650 m) off southern California. It is compared with other species of *Maldane* with a dorsal glandular band or ridge posterior to the neuropodial glandular pad of setiger 5. Features of the cephalic and anal plaques, collar, glands, and patterns in the number of uncini per setiger are discussed. The new species is closest in morphology to *M. cuculligera* Ehlers, 1887 of the Gulf of Mexico and western Atlantic Ocean (about 200 m to 1,000 m depths) and *M. monilata* Fauchald, 1972 from the Middle America and Peru-Chile Trenches (about 1800 m to 3500 m depths). It is hypothesized that these three taxa derived from a common ancestor and that speciation resulted mainly from the uplift of the Panama Isthmus 2 to 3 million years ago.

During descriptive and monitoring surveys off southern California, a new species of *Maldane* Grube, 1860 was collected. The new species may be grouped with several species of *Maldane* that possess a dorsal glandular band or ridge posterior to the neuropodial glandular pad of setiger 5. Remaining species of *Maldane* lack that particular dorsal gland (Green, 1984).

Arwidsson (1907) was the first to describe and illustrate glands for species of the subfamily Maldaninae. However, the use of glands as a taxonomic character was not widely adopted, and most species descriptions and/or discussions lack detail regarding glands. One notable exception is the preanal glandular pads, which commonly are used to define a setigerous preanal segments (Arwidsson, 1907; Ehlers, 1887; Fauchald, 1972; Imajima and Shiraki, 1982). Another exception is that some reports include reference to the dorsal gland posterior to the neuropodial pad of setiger 5 (Arwidsson, 1907; Detinova, 1985; Fauvel, 1914; Green, 1984; Imajima and Shiraki, 1982; Monro, 1937).

Species of *Maldane*, as presently accepted, that possess the above-mentioned dorsal gland include *M. cristata* Treadwell, 1923; *M. cuculligera* Ehlers, 1887; *M. monilata* Fauchald, 1972; and *M. sarsi* Malmgren, 1865. The new species, *M. californiensis*, is described herein, and is compared with those species. Results of those comparisons are used to present a hypothesis regarding the relationship of *M. californiensis* to those species.

METHODS

Biological specimens, including type material, were obtained on loan from the Allan Hancock Foundation, University of Southern California (AHF), polychaetes now property of Los Angeles County Museum of Natural History; Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); National Museum of Natural History, Smithsonian Institution (USNM); Southern California Coastal Water Research Project (SCCWRP); and Texas A&M University, College Station (TAMU). Specimens were examined with dissecting and compound microscopes. Methyl green staining was used to highlight glandular areas. This technique (using methyl green or other stains) has been applied to maldanids (Detinova, 1985; Green, 1987; Monro, 1937) and to other polychaete families (Banse, 1970). Uncini were counted in each setiger on one or both sides of the worm. The number of uncini is essentially the same on both sides of the worm unless there has been damage to the neuropodia (Green, 1984). Counts from undamaged setigers were used in comparisons among specimens of different size. Because some specimens are fragments, width of the body (widest point) rather than length was used as a measure of size. Drawings were made with the aid of microscopes with a drawing tube. Type material is deposited in the AHF and USNM.

Maldane californiensis new species

Figures 1, 2

Material examined.—PACIFIC OCEAN, southern California. San Pedro Basin, 33°23'30"N, 117°54'54"W, at the following BLM/USC stations: 82803, 536 m, holotype (AHF 1496); 82824, 541 m, 1 paratype (AHF 1497); 82801, 543 m, 1 paratype (AHF 1498); 82807, 536 m, 2 paratypes (USNM 136599); 82817, 536 m, 1 specimen (AHF); 82823, 552 m, 1 specimen (AHF). San Pedro Basin Slope, 33°28'12"N, 117°58'12"W, at the following BLM/USC stations: 82707, 504 m, 1 paratype (AHF 1499); 82703, 507 m, 1 specimen (AHF); 82722, 508 m, 1 specimen (AHF). Oceanside, 33°07'N, 117°32'30"W, BLM/USC station 85301, 659 m, 1 specimen (AHF). Point Dume, 33°57'36"N, 118°53'24"W to 33°58'12"N, 118°53'06"W, VELERO IV station 24031, beam trawl, 621–477 m, 2 specimens (AHF). Point Dume, station coordinates unavailable, VELERO IV station 23982, 85 m, 1 specimen (AHF); VELERO IV station 23984, 552 m, 1 specimen (AHF). Coal Oil Point, 34°23'N, 119°57'W, VELERO IV station 23254, 331 m, 1 specimen (AHF). Santa Monica Bay, 33°56'N, 118°46'15"W, at the following SCCWRP stations: C-22, 578 m, 1 specimen (AHF); 5071, C-22, 578 m, 2 specimens (AHF).

Description.—Specimens have 19 setigers. Holotype complete and measures 65 mm long by about 2 mm wide (widest point). Other measured specimens (paratypes and general material) range in size from about 58 mm to 95 mm long by 2 mm to 3 mm wide. Eggs visible through body wall of some individuals. Specimens lack pigmentation in alcohol.

Cephalic plaque elongate (Fig. 1A, B); margin divided, by lateral incisions, into two lateral margins and continuous posterior margin. Protrudes anteriorly from lateral margins rounded to semi-triangular palpode. Nuchal organs on either side of palpode extend to less than half length of lateral margins. Dorsal surface of plaque convex and forms keel, which extends length of plaque. Lateral and posterior margins smooth. Posterior margin forms deep pocket that covers posterior base of plaque and most of dorsal side of presetous annulus (Fig. 1A, B). Cephalic pocket tapers towards attachment point on dorsum; distal margin above plaque nearly four times wider than proximal margin, which attaches to presetous annulus near border of setiger 1.

Margin of anal plaque divided by narrow (longer than wide) lateral notches (Fig. 1C, D). Dorsal margin smooth and spade-like in shape. Ventral margin deeper than dorsal margin, and slightly crenulate. Anus dorsal; posterior margin of anus raised and covers anal opening (in Fig. 1C, shown above margin of plaque on right side of drawing).

Five internal septa present and separate anterior six setigers. Paired nephridiopores open on ventrum of setigers 7–9 (in Fig. 1E, shown as small circles on ventrum of last three setigers).

Ventral collar present on first setiger (in Fig. 1A, shown as unshaded area to left of notopodial setae).

Glands most developed on setigers 1–6, mainly restricted to neuropodial tori in posterior setigers, and found in two preanal lateral pads. Second preanal pad extends across dorsum; dorso-lateral surface of body is slightly indented below the second pad (in Fig. 1C, preanal pads shown as unshaded dorso-lateral areas between last setiger and dorsal anus).

Glands distributed on anterior setigers as illustrated in Figure 1E, in which shading indicates methyl green staining pattern. Uptake of stain differs along body, with some areas staining lighter or darker. Areas of darkest stain occur on ventro-lateral regions of setigers 3–6. Setigers 1–3 completely biannulate with asetous and setous annuli, and completely glandular. Setigers 4–6 incompletely divided. On ventrum, distinct setous (contain neurosetae) and asetous pads present, and glandular. Distinct segmental lines generally lacking on dorsum. One exception is the complete asetous annulus anterior to setous pad of setiger 4. That asetous

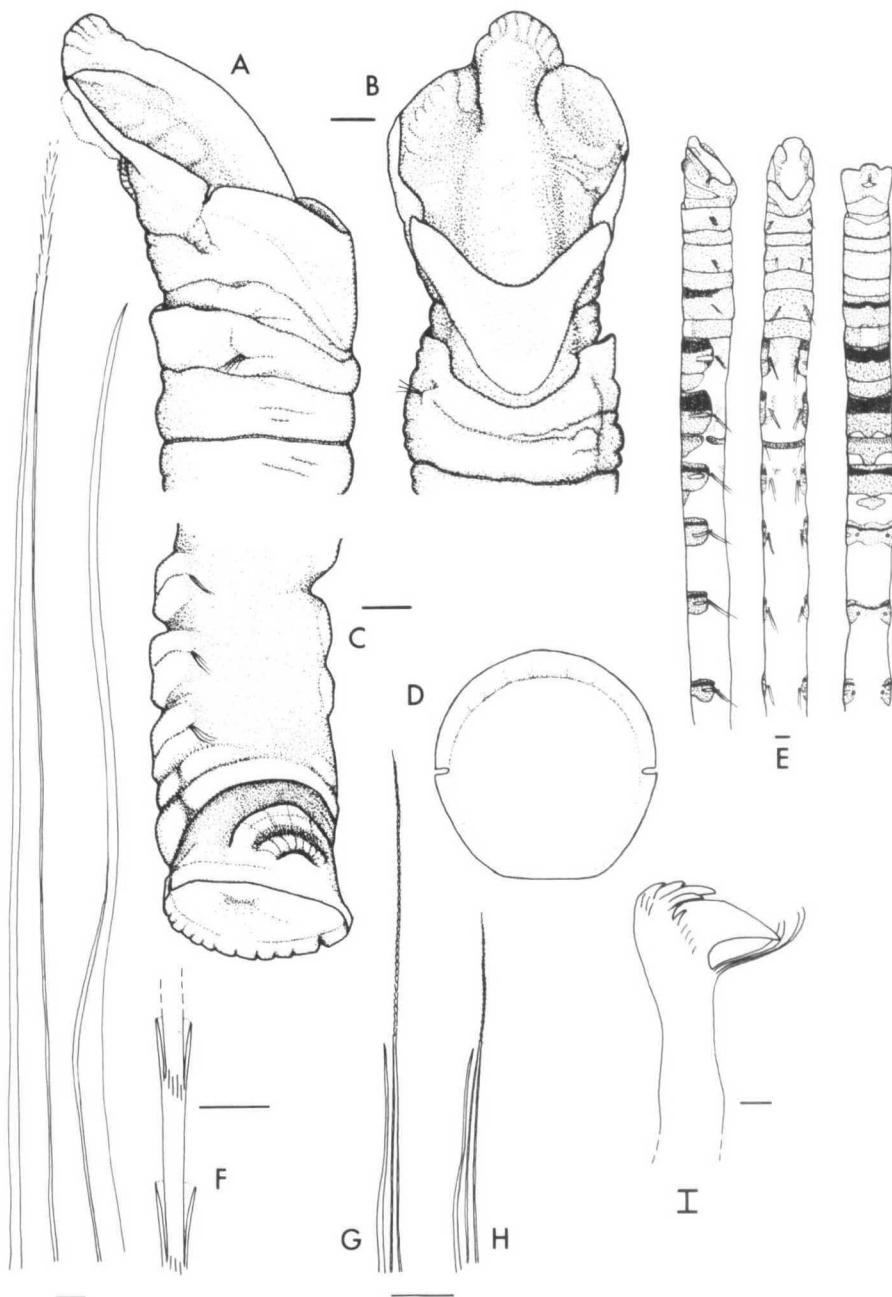


Figure 1. *Maldane californiensis*: A, Cephalic plaque and first setiger, lateral view, ventral collar unshaded and to left of notopodia; B, Cephalic plaque, top view; C, Anal plaque and setigers 17-19, dorso-lateral view, glandular areas unshaded on neuropodial tori and on preanal pads below last setiger; D, Anal plaque, bottom view, dorsal side down; E, Anterior nine setigers, shading indicates methyl green staining pattern on lateral (drawing on left), dorsal (drawing at center), and ventral (drawing on right) sides of body; F, Notosetae, setiger 13, bilimbate seta with haired tip (entire tip not shown) (left), geniculate seta (center), and detail of haired portion of bilimbate seta (right); G, geniculate (left) and bilimbate setae (right), setiger 6; H, geniculate (left) and bilimbate setae (right), setiger 18; I, Neuroseta, setiger 15. Line scales are 1.0 mm for A-E, 0.1 mm for G, H, and 0.01 mm for F and I. Drawings A-C from holotype (AHF 1496); drawings D-I from specimens from Santa Monica Bay, stations 5071 and C-22.

annulus glandular except for small non-glandular (unstained) patch on ventrum. With exception of some diffuse patches of glands between notopodia of setigers 4–6, dorsum largely non-glandular from setous annulus of setiger 4 to end of worm. Noteworthy exception is a dorsal glandular band or ridge, which occurs in line with ventral asetous glandular pad, located posterior to neuropodial glandular pad of setiger 5.

Muscular bands between the tori of setigers 6–19 on lateral sides of body. Bands not glandular; do not stain with methyl green.

Setiger 1 uniramous and lacks neurosetae. Setigers 2–19 biramous. Setaal fascicles lateral and near middle of setous annuli or tori pads.

Notosetae of setigers 2–19 in anterior and posterior rows; anterior row near the ventral portion of fascicle. Setae of anterior row slightly geniculate (Fig. 1F, center). Setae of posterior row bilimbate and distal portion "haired" (Fig. 1F, left). Distal margin appears fimbriated and regularly divided along shaft into wing-like flaps (Fig. 1F, right). Bilimbate setae longer than geniculate setae; about two times longer in setigers 6–16 (Fig. 1G) and less than that in setigers 2–5 and 17–19 (Fig. 1H). Greater length in median setigers related to haired portion of seta, which ranges from about $\frac{1}{2}$ to $\frac{2}{3}$ length of shaft in setigers 6–16 (Fig. 1G) to less than $\frac{1}{2}$ length of shaft in setigers 2–5 and 17–19 (Fig. 1H).

Notosetae on setiger 1 different from setae on setigers 2–19. Setae crowded together and not in distinct rows. Geniculate and bilimbate setae of similar length. Finally, distal portion of the bilimbate setae not obviously haired.

Rostrate uncini present in neuropodia of setigers 2–19 (Fig. 1I). Number of uncini per setiger varies along body in similar fashion for adult worms of different size (Fig. 2, top two graphs). Specimens 2 mm to 2.5 mm wide (N = 4) with 13–17 uncini on setiger 4, 32–40 uncini on setiger 5, 27–32 uncini on setiger 6, and 23–31 uncini on setigers 7 through 19. Specimens 2.5 mm to 3 mm wide (N = 2) with 16–18 uncini on setiger 4, 41–46 uncini on setiger 5, 37–38 uncini on setiger 6, and 34–37 uncini on setigers 7 through 19. Although number of uncini per setiger generally increases with size of worm, pattern of change in number of uncini along body is similar among worms of different size. Considering worms from 2 mm to 3 mm wide, uncini pattern described as relatively large increase of 19–27 uncini from setiger 4 to 5, moderate decrease of 6–11 uncini from setiger 5 through 7, and similar number of uncini from setigers 7 through 19. Because several of the worms had eggs, the above-described pattern is for adult worms. Smaller individuals were unavailable for comparison.

Distribution.—Pacific Ocean off southern California from Coal Oil Point to Ocean-side. Collected from silty clays and soupy muds (BLM/USC designations) from depths of 331 m to 659 m; one record from 85 m.

Remarks.—Off southern California, *M. californiensis* may co-occur with *M. sarsi* (author's observation). (I consider *M. cristata* and *M. sarsi* records off California as equivalent and prefer to refer to the taxa as *M. sarsi*; Green, 1984.) *Maldane sarsi* resembles *M. californiensis* in general appearance of the cephalic and anal plaques, and both species possess a dorsal gland posterior to the neuropodial pad of setiger 5. In contrast to *M. californiensis*, *M. sarsi* lacks a collar on the first setiger. Other differences between the species concern the development of some of the glands and the pattern of change in the number of uncini per setiger. The ventral asetous glandular pad posterior to the neuropodial glandular pad of setiger 6 is larger (extends between neuropodial pads of setigers 6 and 7) and rectangular in shape in *M. sarsi*, rather than small and semi-elliptical in shape as in *M. californiensis*. Further, the second preanal glandular pad extends across the dorsum

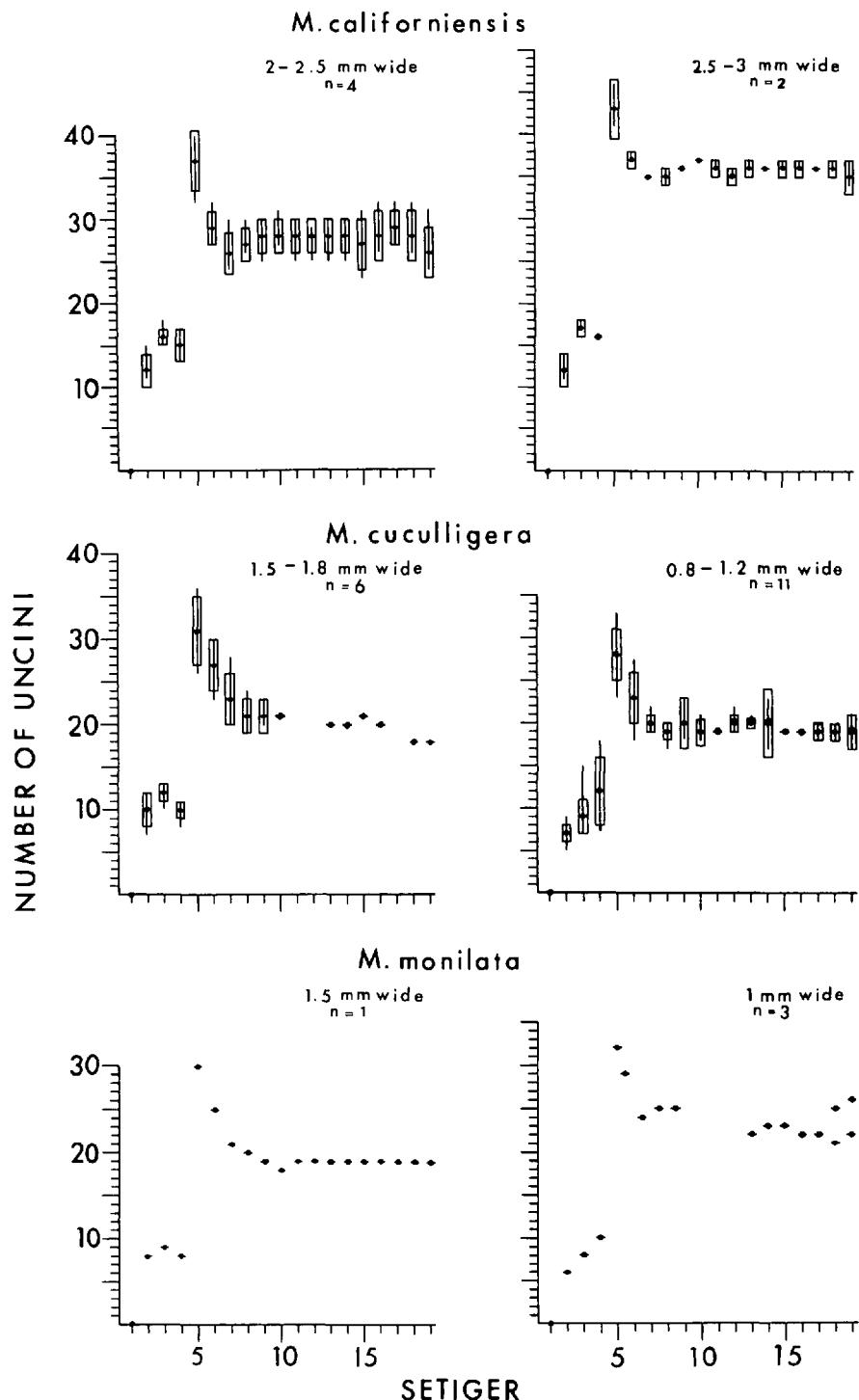


Figure 2. Plots of the number of uncini per setiger (per torus) for different size specimens of *M. californiensis*, *M. cuculligera*, and *M. monilata*. Specimens of the same size were not available for all species, but specimens of the most similar size are lined up on the left. Figures on the right show variation for available smaller or larger specimens. Mean number of uncini per torus indicated by circles, ranges indicated by vertical lines, and standard deviations by boxes. N = number of specimens.

in *M. californiensis*, whereas neither pad extends across the dorsum in *M. sarsi*. The number of uncini moderately decrease (6–11 uncini) from setiger 5 through 7 in *M. californiensis*, whereas they are similar or only slightly decrease (0–4 uncini) from setiger 5 through 7 in *M. sarsi*; comparison based on specimens ranging in size from 2 mm to 3 mm wide. Specimens of *M. sarsi* (from southern California) 2 mm to 3 mm wide (N = 6) with 8–16 uncini on setiger 4, 24–33 uncini on setiger 5, 24–31 uncini on setiger 6, 23–30 uncini on setiger 7, and 20–31 uncini on setigers 8–19; the number of uncini may increase or decrease between setigers 8 and 19 (Green, 1984).

Maldane californiensis is closest in morphology to *M. cuculligera* Ehlers, 1887 of the Gulf of Mexico and western Atlantic Ocean and to *M. monilata* Fauchald, 1972 from the Middle America and Peru-Chile Trenches. Besides the dorsal gland posterior to the neuropodial pad of setiger 5, all three species possess a collar on setiger 1. In addition, the pattern in the number of uncini per setiger is similar among these species (Fig. 2).

Type and non-type specimens of *M. cuculligera* and *M. monilata* were examined, and comparisons are based on those examinations (for additional detail, see the individual sections on *M. cuculligera* and *M. monilata* that follow this remarks section). Briefly, *M. californiensis* resembles most *M. cuculligera*. The species differ in the shape of the dorsal margin of the anal plaque and there are subtle differences in the glands. The dorsal margin of the anal plaque is broadly rounded or flared in *M. cuculligera*, whereas it is spade-like in shape in *M. californiensis*. The ventral asetous glandular pad posterior to the neuropodial glandular pad of setiger 6 is square to rectangular in shape in *M. cuculligera*, rather than semi-elliptical as in *M. californiensis*. An additional feature of the glands deserves mention. In several of the examined specimens of *M. cuculligera*, the dorsal gland and ventral glandular pad posterior to setiger 5 forms a pseudocollar. Such a condition has not been observed in *M. californiensis* or *M. monilata*. The relatively greater development of those dorsal and ventral glands in *M. cuculligera* deserves further study; not enough specimens of the three species have been examined to document the degree of variation in this character.

M. monilata differs from *M. californiensis* and *M. cuculligera* by having an entire or dorso-ventral collar on setiger 1. Further, *M. monilata* differs with regard to features of the cephalic and anal plaques. The presetous annulus separates the cephalic pocket from setiger 1 in *M. monilata*, whereas the pocket is adjacent to the first setiger in *M. californiensis* and in *M. cuculligera*. Further, the cephalic pocket is not as tapered in *M. monilata* as it is in *M. californiensis* and *M. cuculligera*. The dorsal margin of the anal plaque is tapered in *M. monilata*, rather than spade-like or rounded as in *M. californiensis* and *M. cuculligera*, respectively. Finally, the lateral notches on the anal plaque appear more developed because they are nearly as wide as they are long in *M. monilata*, whereas they are longer than wide in *M. californiensis* and in *M. cuculligera*.

The close relationship among *M. californiensis*, *M. cuculligera*, and *M. monilata* initially was discussed by Green (1984). In that unpublished thesis, *M. californiensis* (identified as sp. A), and *M. monilata* were referred to as subspecies of *M. cuculligera*. This was done to emphasize their relationship and to distinguish it from other species complexes of *Maldane* identified in that manuscript. That approach is abandoned in this paper and the three taxa are considered distinct species.

Maldane cuculligera Ehlers, 1887
Figures 2, 3

Maldane cuculligera Ehlers, 1887: 178–182, pl. 46, figs. 1–9.

Material Examined.—GULF OF MEXICO. 28°47'30"N, 88°47'30"W, Gulf Stream and Gulf of Mexico Exploration 1877–1878, BLAKE station 48, 974 m, 1 lectotype and 29 paralectotypes (MCZ 771); 29°30'18"N, 86°52'24"W, station 67A5-13B, 379 m, 4 specimens (TAMU 1-0276); 28°51'N, 88°47'30"W, station 67A7-1A, 850–520 m, 2 specimens (TAMU 1-0277); 28°56'N, 88°42'W, station 67A7-2A, 408 m, 2 specimens (TAMU 1-0278); 28°58'N, 88°28'W, station 69A13-44, 751 m, 3 specimens (TAMU 1-0279).

Remarks.—Type material consists of 30 anterior and 10 posterior fragments. All specimens are in poor condition due to dehydration; label in jar noted that the material was found without alcohol 26 March 1897. A lectotype anterior and posterior fragment is designated, as follows: anterior fragment consists of eight setigers and is 13 mm long by 2 mm wide (widest point); posterior fragment consists of six setigers (partially enclosed in a silty tube) that measure 11 mm long by 0.8 mm wide. Other type specimens range from about 10 mm long by 0.8 mm wide for seven setigers to about 14 mm long by 1.8 mm wide for five setigers. One of the non-type specimens is complete with 19 setigers, and is 60 mm long by 1 mm wide (TAMU 1-0276).

Cephalic and anal plaques are as described and figured by Ehlers (1887), although the cephalic palpode and keel of the type material are now misshapen due to dehydration (Fig. 3A–D). Of particular note is that the posterior margin of the cephalic plaque forms a deep pocket that tapers towards its attachment, which is on the presetous annulus near the border of setiger 1.

The dorsal margin of the anal plaque is smooth; it may be flared as in the type material (Fig. 3C, D), which is consistent with Ehlers' (1887) drawing, or it may be broadly rounded (TAMU specimens). The ventral margin is smooth to slightly crenulate.

A ventral collar is on the first setiger (in Fig. 3A, unshaded area to left of notopodia).

Glands are difficult to discern in the type material due to dehydration. However, the dorsal glandular band and ventral asetous glandular pad overlaps and encircles the body at the base of the neuropodial pad of setiger 5 (Fig. 3E). This feature has been referred to as a collar (Ehlers, 1887; Fauchald, 1972). However, the collar-like appearance of these glands more likely is the result of contraction of the worm, as suggested by Augener (1906). In some of the TAMU specimens, the dorsal gland is ridge-like, but it and the ventral gland do not form a deep pseudocollar. Glands are similar to those in *M. californiensis*. A noteworthy exception, observed in the TAMU specimens, is that the ventral asetous glandular pad posterior to the neuropodial glandular pad of setiger 6 is square to rectangular in shape.

Notosetae of *M. cuculligera* are like those in *M. californiensis*. The pattern in the number of uncini per setiger may be described as a relatively large increase of 14–21 uncini from setiger 4 to 5, a moderate decrease of 6–10 uncini from setiger 5 through 7, and a similar number of uncini from setigers 7 through 19 (Fig. 2, center graphs). Specimens ranging in size from 0.8 mm to 1.8 mm wide (N = 17, mainly fragments), with 7–18 uncini on setiger 4, 23–36 uncini on setiger 5, 18–30 uncini on setiger 6, and 17–28 uncini on setigers 7 through 19.

Specimens examined from the Gulf of Mexico were collected from depths of 379 m to 974 m. Augener (1906) reported *M. cuculligera* in the western Atlantic from off Grenada, Delaware, and New Jersey from depths of 232 m to 1,332 m. He did not fully describe nor figure the specimens. Those records have not been confirmed by the author. However, an anterior fragment (6 setigers) of a *M. cuculligera*-type of specimen was examined that had been collected from off Dutch Guiana, now known as Surinam (07°52'N, 54°31'30"W to 07°55'N, 54°35'W, chain

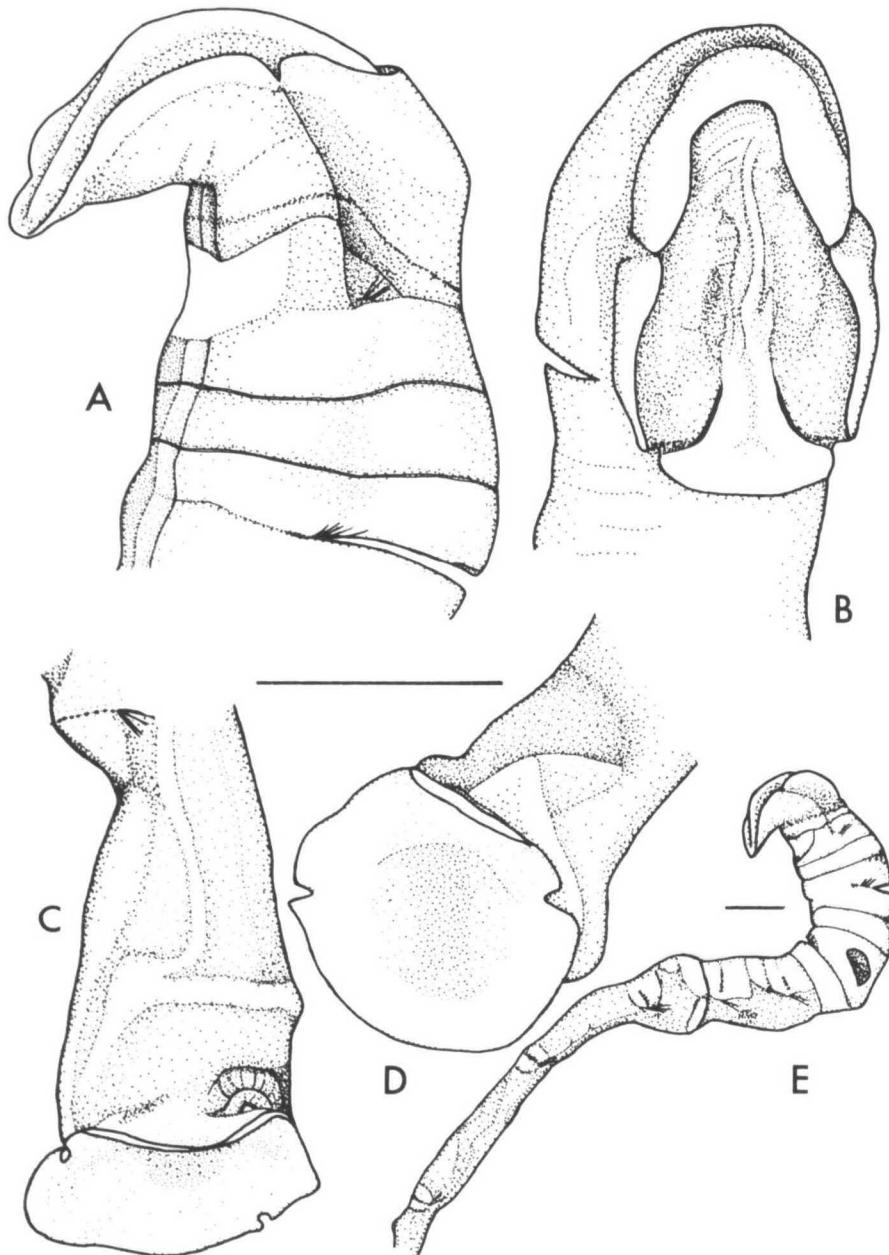


Figure 3. *Maldane cuculligera*: A, Cephalic plaque and first setiger, lateral view, ventral collar unshaded and to left of notosetae; B, Cephalic plaque, top view, keel shriveled due to prior dehydration; C, Anal plaque and setiger 19, dorso-lateral view, preanal glandular pads not figured due to poor condition of specimen; D, Anal plaque, bottom view, dorsal side up; E, Anterior eight setigers, lateral view, ventral collar on setiger 1 outlined, glandular areas unshaded on setigers 2-6, darkly shaded area on setiger 3 indicates tear in body where setae are missing. Line scales are 1.0 mm. Drawings from lectotype (MCZ 771).

dredge 33, 1 specimen, AHF), which is close to the reported occurrence off Grenada.

Maldane monilata Fauchald, 1972
Figures 2, 4

Maldane monilata Fauchald, 1972: 263–265, pl. 54, figs. c–g.

Material Examined.—PACIFIC OCEAN. Mexico, Isla Maria Magdalena, 21°19'30"N, 106°42'00"W, VELERO IV station 11743, 3,188 m, holotype (AHF). Ecuador, 03°45"S, 81°37'W, ANTON BRUUN Station ABII-8, 2,765 m, 6 specimens (AHF).

Remarks.—Holotype is complete with 19 setigers and is 34 mm long by 1.5 mm wide. Other examined specimens were fragments of various lengths by about 1 mm wide.

Cephalic and anal plaques (Fig. 4A–H) are as described by Fauchald (1972). In addition, the posterior margin of the cephalic plaque is attached near the anterior margin of the presetous annulus, which widely separates the cephalic pocket from the first setiger (Fig. 4A, C, D). With regard to the anal plaque, the margins somewhat overlap the lateral notched openings, which are nearly as wide as long. This gives the lateral notches the appearance of being more developed in *M. monilata* than in *M. californiensis* and *M. cuculligera*. The dorsal margin of the plaque is tapered.

The collar on the first setiger exhibits some variation. It may be entire with lateral incisions (Fig. 4A, B), or it is separated into dorsal and ventral halves (Fig. 4C, D). The dorsal portion of the collar may be indented or is divided into two lobes (as in the holotype). The ventral portion of the collar may be slightly indented.

Glands were not described by Fauchald (1972). They are similar to *M. californiensis* with the following exception. The neuropodial glandular pad of setiger 6 is square to rectangular in shape, rather than semi-elliptical in shape as in *M. californiensis*. There are two preanal glandular pads; not one preanal segment as described by Fauchald (1972). Like *M. californiensis*, the second preanal pad extends across the dorsum.

Notosetae are like those described for *M. californiensis*; they are not finely bilimbate throughout as described by Fauchald (1972). The pattern of the number of uncini per setiger may be described as a relatively large increase of 22 uncini from setiger 4 to 5, a moderate decrease of 8–9 uncini from setiger 5 through 7, and a similar number of uncini from setigers 7 through 19 (Fig. 2, bottom graphs). Specimens ranging in size from 1 mm to 1.5 mm wide (N = 4), with 8–10 uncini on setiger 4, 30–32 uncini on setiger 5, 25–29 uncini on setiger 6, and 19–26 uncini on setigers 7 through 19.

Maldane monilata presently is known from the Middle America Trench from the Gulf of California to Panama and from the northern extent of the Peru-Chile Trench off Ecuador. Collections have been reported from depths of 1,865 m to 3,511 m (Fauchald, 1972).

DISCUSSION

Morphological characters of most use in describing *M. californiensis* and in comparing it with other species include the cephalic and anal plaques, collar, glands, and pattern in the number of uncini per setiger. Features of the cephalic and anal plaques and the presence/absence of a collar are conventional taxonomic characters for maldanids (Fauchald, 1977a). However, features of the cephalic plaque considered most useful in this paper usually are not mentioned; these

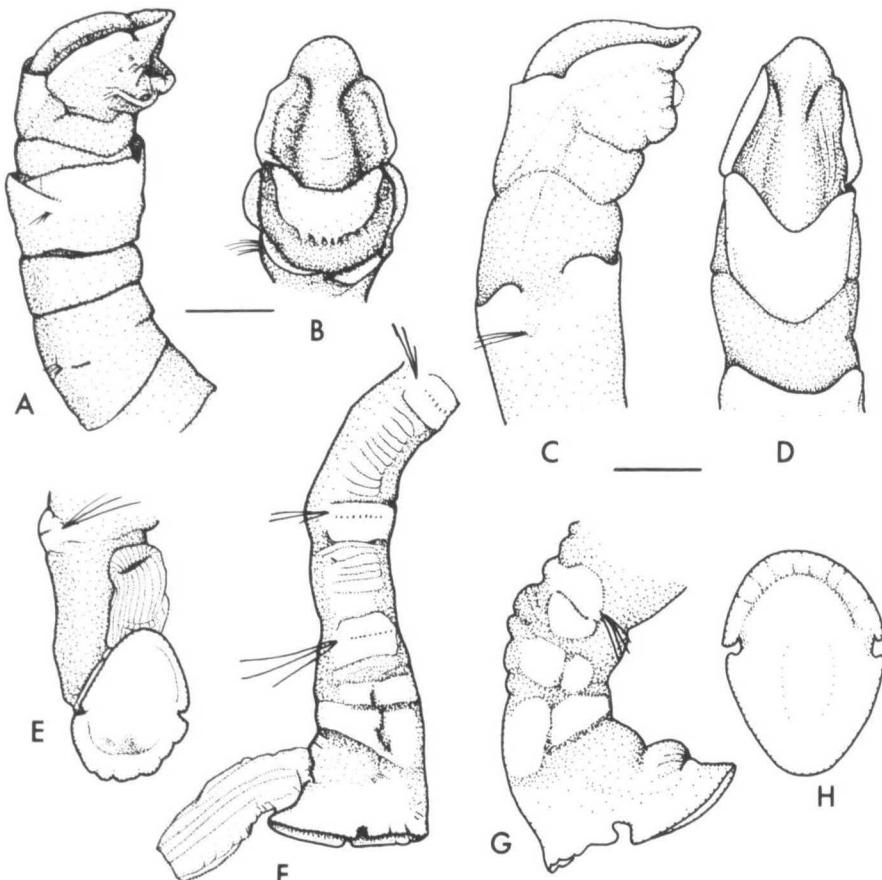


Figure 4. *Maldane monilata*: A, Cephalic plaque and first two setigers, lateral view; B, Cephalic plaque, top view; C, Cephalic plaque and first setiger, lateral view; D, Cephalic plaque, top view; E, Anal plaque, bottom view; F, Anal plaque and setigers 17-19, anus prolapsed, lateral view; G, Anal plaque and setiger 19, lateral view; H, Anal plaque, bottom view. Line scales are 1.0 mm. Drawings A, B and E, F from holotype (AHF); drawings C, D and G, H from specimen ABII-8 (AHF).

include the shape of the cephalic pocket and the location of its attachment on the dorsum. It is suggested that the taxonomic use of these characters be considered in future descriptions.

As mentioned in the introduction, only a couple of features of the glands have received attention in the literature. These include the presence of a dorsal gland posterior to the neuropodial pad of setiger 5 and the number of preanal glandular pads. Other features of the glands are less well known. In general, glandular development is similar among the taxa compared in this paper. Features that did vary among the species include the shape of the ventral asetous glandular pad posterior to the neuropodial pad of setiger 6, and the dorso-lateral extent of the preanal glandular pads. These results indicate that closer attention should be given to the shape and/or development of the glands. I suggest that further study of the glands along the body is needed before their full potential as taxonomic characters can be realized.

Counts of the number of uncini per setiger are not commonly reported, although they have been included in descriptions of *Maldane* by Arwidsson (1907) and

Green (1984) and for other maldanids by Green (1987) and Pilgrim (1977). Detinova (1985) considers the change in the number of uncini from setiger 4 to 5 of taxonomic importance in separating selected species of maldaninae. I feel that the change in the number of uncini along the entire body (uncini pattern) is more informative (Green, 1984, 1987).

Results presented herein suggest that uncini patterns are useful as a taxonomic character. There is correspondence between uncini patterns and more conventional features of morphology. For example, widely distributed *M. californiensis*, *M. cuculligera*, and *M. monilata* possess a collar on the first setiger, and the uncini pattern is similar among these taxa. The presence/absence of a collar also is useful for distinguishing *M. californiensis* and *M. sarsi*, which may have a sympatric occurrence off California. In contrast to *M. californiensis*, *M. sarsi* lacks a collar; and the uncini patterns for these species are different.

M. californiensis is considered most closely related to *M. cuculligera* and *M. monilata*. That relationship is supported by an overall similarity in the glands including the presence of a dorsal gland posterior to the neuropodial pad of setiger 5; presence of a collar on the first setiger; and an uncini pattern characterized as a relatively large increase of 14–27 uncini from setiger 4 to 5, a moderate decrease of 6–11 uncini from setiger 5 through 7, and a similar number of uncini on setigers 7–19. No other species of *Maldane* share this combination of characters (Green, 1984).

Given the close relationship between the three species, it is of interest to note that the uncini patterns are similar over a wide range of specimen sizes. When one considers the combined specimens of *M. californiensis*, *M. cuculligera*, and *M. monilata*, the size range of the examined specimens is from 0.8 mm to 3 mm wide. Although the number of uncini per setiger increases with size of the worm, the magnitude of change in the number of uncini between setigers is similar across the above-specified size range. Specimens smaller than 0.8 mm wide were not examined, and it is not known how reliable uncini patterns would be for very small individuals.

M. californiensis appears most closely allied to *M. cuculligera*. For both species the collar on the first setiger is ventral. In addition, the cephalic plaques are nearly identical; the posterior margin acutely tapers towards its attachment on the presetous annulus near the border of setiger 1. The two species differ in that the dorsal margin of the anal plaque is spade-like in shape in *M. californiensis*, whereas it is broadly rounded or flared in *M. cuculligera*. Further, the ventral asetous glandular pad posterior to the neuropodial pad of setiger 6 is square to rectangular in shape in *M. cuculligera*, and is semi-elliptical in *M. californiensis*.

Maldane monilata is the most different of the three species. It has a complete or dorso-ventral collar on the first setiger. The dorsal margin of the anal plaque is tapered and the lateral notches appear more developed. Further, the posterior margin of the cephalic plaque is not acutely tapered and it is separated from setiger 1 by the presetous annulus.

Besides morphology, *M. californiensis* also is more similar to *M. cuculligera* in regards to habitat. The depth ranges of *M. californiensis* and *M. cuculligera* somewhat overlap (about 85 m to 650 m and about 300 m to 1,000 m, respectively). In contrast, *M. monilata* occurs in abyssal depths (about 1,800 m to 3,500 m).

The geographic ranges for the species provides the only deviation from the generally closer relationship between *M. californiensis* and *M. cuculligera*. That is *M. californiensis* and *M. monilata* occur in the Pacific Ocean and *M. cuculligera* occurs in the Gulf of Mexico and western Atlantic.

That deviation may be resolved by consideration of the geological history of the region. The eastern Pacific and western Atlantic were interconnected during the Mesozoic and early Cenozoic eras (Dietz and Holden, 1970). Later they became isolated with the uplift of the Isthmus of Panama two to three million years ago during the late Pliocene-early Pleistocene epochs (Briggs, 1974; Hallam, 1972). Thus, it is plausible that the three species derived from a common ancestor that lived at least two to three million years ago in the sea that separated North and South America.

Speciation then could have resulted, in part, from vicariance of the ancestral population on opposite sides of the Isthmus. This hypothesis provides a mechanism by which *M. cuculligera* and *M. californiensis* could be sister species. To my knowledge, this result would represent the first record of such sister species in polychaetes. At the time of Fauchald's (1977b) paper on Panama polychaetes, he commented that the state of polychaete taxonomy was too primitive to allow recognition of sister species. The above-described mechanism has been recognized as resulting in sister species of crabs, fishes, and molluscs in the Pacific Ocean and the Gulf of Mexico (Briggs, 1974; Hallam, 1972).

It is speculated that *M. monilata* derived from part of the ancestral population that entered the Middle America Trench, created after the uplift of the Isthmus.

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